

A Geographic and Taxonomic Review of *Taningia danae* Joubin, 1931 (Cephalopoda: Octopoteuthidae), with New Records and Observations on Bioluminescence

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Abstract: The capture of a very large deep-sea squid, *Taningia danae* Joubin, 1931 by a commercial trawl in Georges Basin, western North Atlantic, prompted a study of the nomenclature and distribution of the species as reported in the literature. The previously published records indicate a world-wide warmwater distribution excluding the western North Atlantic, Caribbean Sea, Mediterranean Sea, and central Pacific. The Georges Basin specimen, the largest recorded *T. danae* (mature female, 160 cm mantle length), together with 16 smaller specimens caught in midwater trawls and deposited in the collections of the National Museum of Natural History (NMNH), extend the known distribution into the western North Atlantic. Additional specimens in the NMNH collections also fill in the distribution in the central North Pacific. Observations of bioluminescent flashes from the arm-tip photophores of a live specimen captured off Hawaii are reported for the first time. Early reports of various species of *Cucoteuthis* Steenstrup, 1882 and the original description of *C. unguiculata* (Molina, 1782) may represent *T. danae* but lack sufficient detail for verification of identification to genus or species.

Introduction

The deep-sea squid *Taningia danae* Joubin, 1931 is recognized as a cosmopolitan, primarily tropical to subtropical species that ventures into boreal waters (Nesis, 1987; Okutani and Clarke, 1985; Roper *et al.*, 1985). The species has been recorded from some regions of all oceans, but it has not been documented from the western North Atlantic, even though it is widespread and abundant in the eastern North Atlantic. Nor has it been found in the tropical western Atlantic, the Mediterranean, or the central Pacific.

The small holotype was captured in the eastern Atlantic in a small-mesh pelagic fishnet by the research vessel *Dana* in 1921, and subsequently a few other plankton net or midwater trawl captures were recorded (e.g., Lu and Clarke, 1975a, b; Okutani, 1974). However, the vast majority of specimens, including almost all large ones, have come from the stomachs of predators, principally sperm whales. A few also have been taken from stomachs of sharks, lancetfishes, tunas, wandering albatross and elephant seals. A very small number of large specimens found floating dead at the surface are presumed to have been regurgitated from sperm whales.

Previous records show that nets catch the smallest specimens and sperm whales catch the largest, up to a total length in excess of 2m. Curiously, the larger fishing gear, both commercial and biological mid-water trawls and benthic otter trawls, seem not to have captured *T. danae*. Are the large adults so quick and agile that they can avoid capture by nets, or do they live in association with a habitat where nets normally cannot be fished?

This paper reports specimens of *T. danae* from the western North Atlantic and the central Pacific. One very large specimen of 160 cm mantle length (ML) was captured in a commercial otter trawl just north of Georges Bank off Massachusetts, USA, and 16 paralarval and juvenile specimens, captured in fine-mesh Isaacs-Kidd Midwater Trawls, are recorded from the waters off Bermuda. In addition, a number of small specimens are listed from other regions, e.g., off St. Helena and Gough Islands in the South Atlantic, in the north central North Pacific, off Hawaii, and in the western South Pacific east of New Zealand. All specimens reported here were captured by nets.

In addition, the convoluted taxonomic history of the species is reviewed, as well as the geographical distribution and aspects of its biology. Observations of the bioluminescent flashes produced by the

photophores on the tips of arms II are reported.

Historical Review

Taningia danae was described by Joubin (1931) based on a single small specimen of 68 mm total length, about 40 mm ML. The specimen was captured during the 1921 *Dana* Expedition west of the Cape Verde Islands (14°52'N 28°04'W) in an open 2 m small mesh (stramen) net fished at a depth of 100 m. While Joubin recognized the new species as belonging to the Octopodoteuthidae (= Octopoteuthidae), he felt that the pair of large photophores on the tips of arms II were so distinctive as to warrant the erection of a new genus. The description and illustrations are quite detailed and comprehensive because the specimen was in excellent condition. The holotype is deposited in the Zoologisk Museum, University of Copenhagen, Denmark.

It has been suggested that the spelling of the generic name should be emended to "*Taaningia*" because when naming the genus for Vedel Tåning, Joubin incorrectly transliterated the diacritic mark. Although diacritic marks are not permitted by Article 27 of the International Code of Zoological Nomenclature and "å" is properly transliterated as "aa", Article 32 of the Code states that the original spelling is incorrect if

"there is in the original publication itself, without recourse to any external source of information, clear evidence of an inadvertent error, such as lapsus calami or a copyist's or printer's error (incorrect transliteration or latinization and use of an inappropriate connecting vowel are not to be considered inadvertent errors)."

Therefore, if the incorrect transliteration was what Joubin intended and not, for example, a printer's error, the original spelling is to be considered correct. In the original description Joubin (1931, p. 185) stated "Je dédie ce genre nouveau à M. Vedel Tåning,..." including the diacritic, but consistently spelled the genus name *Taningia*. Thus, we do not consider the error to be inadvertent and we retain the original spelling.

Joubin noted a similarity in the large fins of *Taningia* to those of the long established *Cucoteuthis* Steenstrup, 1882, but considered the musculature to be distinctive. *Taningia danae* was not reported again until Clarke (1966) gave its distribution based on large specimens previously identified as *Cucoteuthis unguiculatus* (Molina, 1782). Thus M.R. Clarke was the first to recognize that *Taningia danae* was the juvenile form of some specimens that had been called *Cucoteuthis unguiculatus*.

The nomenclatural history of *Cucoteuthis unguiculatus* is complicated and colorful. The original "mangled" specimen was found floating at the surface well off the coast of Chile (30°44'S 110°33'W) during Cook's first voyage on *Endeavour* in 1769. Cook described the arm hooks in his diary, then mentioned that this "cuttlefish" made one of the best soups they had ever tasted (Beaglehole, 1962; *vide* Clarke, 1967). Cook's description and a preserved arm, possibly from the same squid, apparently provided the basis for Molina's description in 1792 of *Sepia unguiculata*, which Orbigny (1834-48: 339) subsequently renamed *Enoploteuthis molina*. Steenstrup (1882) pointed out that Owen's (1881) *Enoploteuthis cooki*, based on a piece of one arm, probably the same piece for which *E. molina* was named, together with other pieces which probably were not from Cook's specimen, was in fact, *E. unguiculata* (Molina). Steenstrup's convoluted analysis resulted in the naming of the new genus *Cucoteuthis*, from the Greek for coco fruit, a reference to the swollen hook sheaths and an honorific name in recognition of Cook.

Several large remnants from the stomach of a "whale" from the "Indian Ocean" were described and figured in detail by Harting (1861) and attributed to *Enoploteuthis*, reminiscent of *E. unguiculata*, but they were not sufficient to allow specific identification. Verrill (1882), however, who apparently felt compelled to tidy up undesigned species, named Harting's specimen *Enoploteuthis Hartingii*.

Clarke (1967) amplified considerably the knowledge about *T. danae* based on 14 specimens, 12 of which were quite large, taken from the stomachs of sperm whales (*Physeter catodon*). He also pointed out that the specimens reported as *Cucoteuthis unguiculatus* by R. Clarke (1956), Rees and Maul (1956), and M.R. Clarke (1962a) are to be regarded as *T. danae*. He also felt that the two specimens reported as *C. unguiculatus* by Joubin (1898, 1900) probably also were *T. danae*, as was the one by Harting (1861), although less certainly so. Clarke gave no reason for assigning priority to *T. danae* rather than *C. unguiculatus*.

Our analysis of the descriptions and illustrations of all earlier references to the species ultimately referred to as *Cucoteuthis unguiculatus*, including Owen's (1881) chimeric reconstruction of *Enoploteuthis cooki*, convinces us that specific and even generic designations cannot be verified, and especially can-

not be positively linked to *Taningia danae*. For example, some could easily be very large specimens of *Octopoteuthis* species. All descriptions and illustrations lack any clear indication of photophores at the arm tips. We concur with Clarke's (1967) assertion that the specimens of R. Clarke (1956), Rees and Maul (1956) and M.R. Clarke (1962a) are *T. danae*, but we are less certain of those of Joubin (1898, 1900) and especially of Harting (1861). We consider *Cuciteuthis* and its included species to be *nomena dubia*.

An additional nomenclatural problem exists from a name applied to a paralarval specimen. Chun (1910: 144) described a paralarva of 4.5 mm ML from the Gulf of Aden as the oldest larva of *Octopoteuthis* (= *Octopoteuthis*). He stated that the arms bear only suckers and that especially noteworthy are the knoblike swellings found only at the tips of arms II. His figures (plate XVII, figs. 1, 2, and 10) clearly show these swellings, undoubtedly precursors of the photophores characteristic of *Taningia*. Naef (1923: 337) recognized this as a species distinct from the known *Octopodoteuthis*, *O. sicula*, and erected the name *O. persica* based on Chun's description and figures. Because this species clearly belongs to *Taningia*, the specific name *persica* has priority over *danae* by eight years. However, the name *O. persica* has not been used in the literature since the original description and only confusion and instability would result from forcing its use. We are applying to the International Commission for Zoological Nomenclature for suppression of *Octopodoteuthis persica* Naef, 1923 under Article 79c (Plenary Powers) of the International Code for Zoological Nomenclature (ICZN). According to Article 80a of the ICZN, existing usage, defined as "the most current usage", of a name under consideration by the Commission is to be maintained. Thus, *T. danae* is to be used rather than *Taningia persica*.

We are left mostly with the "modern" records for *T. danae* to determine its geographical distribution and other aspects of its biology. *Taningia danae* grows to a large size, well over 2 m in total length, and all published records report these large specimens not from nets but from the stomachs of predators, mostly sperm whales, or floating at the surface after being regurgitated by sperm whales. Our material expands the knowledge of this species through a number of specimens collected by a variety of nets, not predators.

Material Examined

Western North Atlantic Ocean: 1F 160 cm ML (frozen), Georges Basin 42°25'N 67°25'W, 0–260m, F/V *Defender*, 7 Dec 1990, USNM 817770. 2J 8–10 mm ML, Bermuda 31°56'N 64°25'W, 55m USNS *Sands* sta 10-9-A, 3 Jun 1970, USNM 726980. 1J 9 mm ML, Bermuda 32°04'N 64°15'W, 0–180m, USNS *Sands* sta 9-3-N, 17 Mar 1969, USNM 726981. 3J 5–8 mm ML, Bermuda 31°45'N 64°17'W, 0–140m, USNS *Sands* sta 9-5-N, 17 Mar 1969, USNM 726982. 1J 8 mm ML, Bermuda 32°10'N 64°08'W, 0–100m, R/V *Trident* sta 4-30-N, 8 Sep 1968, USNM 726983. 1J 15 mm ML, Bermuda 32°00'N 64°23'W, 175m, R/V *Trident* sta 4-5-C, 4 Sep 1968, USNM 726984. 1J 8 mm ML, Bermuda 32°08'N 64°11'W, 120m, R/V *Trident* sta 4-29-C, 8 Sep 1968, USNM 726985. 1J 12 mm ML, Bermuda 32°12'N 64°14'W, 0–100m, R/V *Trident* sta 4-23-M, 7 Sep 1968, USNM 726986. 1J 10 mm ML, Bermuda 32°00'N 64°04'W, 230m, R/V *Trident* sta 4-10-C, 5 Sep 1968, USNM 726987. 1J 6 mm ML, Bermuda 31°53'N 64°22'W, 0–400m, R/V *Sands* sta 9-6-N, 17 Mar 1970, USNM 728036. 1J 8 mm ML, Bermuda 31°51'N 63°47'W, 193–201m, USNS *Sands* sta 13-14-B, 26 Feb 1972, USNM 728037. 1J 8 mm ML, Bermuda 31°55'N 63°51'W, 150–167m, USNS *Sands* sta 13-22-B, 28 Feb 1972, USNM 728038. 1M 14 mm ML, Bermuda 32°10'N 63°59'W, 282–298m, USNS *Sands* sta 14-2-C, 4 Jun 1972, USNM 728039. 1M 26 mm ML, Bermuda 32°17'N 64°17'W, 0–600m, R/V *Delaware* II sta 12-85-N, 24 Aug 1971, USNM 728849.

Eastern North Atlantic Ocean: 1M 41 mm ML, off Madeira Island 34°48'N 20°36'W, 0–230m, R/V *Atlantis II* sta RHB-1914, 24 Jun 1969. 1F 123 mm ML, Cape Verde Islands 10°52'N 22°09'W, 0–608m, R/V *Walther Herwig* sta 490-II-71, 15 Apr 1971, USNM 816681. 1J 20 mm ML, Madeira Island 33°06'N 17°46'W, 0–170m, R/V *Atlantis II* sta RHB-1903, 22 Jun 1969, USNM 817210. 1F 60 mm ML, Cape Verde Islands 10°50'N 22°08'W, 0–(100–111)m, R/V *Walther Herwig* sta 490-I-71, 15 Apr 1971.

South Atlantic Ocean: 1J 20 mm ML, St. Helena Island 15°57'S 05°42'W, A. Loveridge, 17 June 1964, USNM 575748. 1F 110 mm ML, 39°19'S 48°02'W, 0–200m, R/V *Walther Herwig* sta 354-II-71, 6 Mar 1971, USNM 817618. 2F 43–74 mm ML, Gough Island 40°02'S 07°28'W, 0–320m, R/V *Walther Herwig* sta 402-II-71, 18 Mar 1971. 1J 21 mm ML, 40°18'S 39°04'W, 0–800m, R/V *WALTHER HERWIG* sta 363-III-71, 8 Mar 1971.

North Pacific Ocean: 1F 62 mm ML, North Pacific 41°08'N 172°22'W, 0–548m, R/V *Hugh M. Smith*

sta 30-48, 4 Aug 1955, USNM 730681, 1? ca 60 mm ML, Hawaiian Islands approx. 21°30'N 158°20'W, 0-250m, pers. obs. R.E. Young and C.F.E. Roper, 28 Sep 1975, USNM 815476.

South Pacific Ocean: 1F 38 mm ML, New Zealand 39°15'S 179°35'E, 0-(2178-2489)m, USNS *Eltanin* sta 1402, 30 Nov 1964, USNM 817411.

Observations

Georges Basin Specimen.

The fishing vessel *Defender* from Rockland, Maine captured a very large squid while ground-fishing in Georges Basin (42°25'N 67°25'W) on 7 December, 1990 during daytime. The squid was still alive when the mixed catch of pollack, hake, and other ground-fish species was dumped into the below-deck fish hold. The otter trawl had fished on the bottom at about 260m. Because the squid was still alive and virtually undamaged, it probably was captured near the end of the tow or during haul-back. The squid was "pretty weak" and as it was such a large and unusual-looking squid (Capt. James Dow, pers. comm.), it was kept and iced down until the catch was landed in Gloucester, Massachusetts on 10 December 1990. The squid was turned over to biologists of the National Marine Fisheries Service Laboratory in Gloucester. After a series of photographs and a videotape were made, the squid was wrapped in polyethylene sheeting and frozen.

The frozen specimen was brought to the National Museum of Natural History, Smithsonian Institution, in April 1991 where it was examined and measured. This excellent specimen remained frozen until it could be exhibited in the NMNH. The standard series of measurements could not be taken on the frozen specimen with the exception of the following:

Mantle Length (ML)	160 cm
Approximate Total Length	230 cm

After capture and before freezing the specimen weighed 61.4 kg (135 pounds). The specimen is a rich maroon color with pigment nearly evenly distributed over the animal, only slightly darker dorsally (Fig. 1). The tentacles of *Taningia danae* typically cease development and are lost at a ML of about 40-45 mm, so adults are left with 8 arms on which relatively large chitinous hooks occur in two rows, replacing the suckers (Fig. 2). A large, oblong photophore occurs at the tip of each dorsolateral arm (Fig. 1). Darkly pigmented externally, the photophore has a longitudinal slit along the oral surface that opens like an eyelid to expose the creamy white, crenulate light producing surface of the organ (see discussion of bioluminescence below).

Photographs of the specimen reveal the swollen nidamental glands that extend nearly to the mantle opening (Fig. 3), indicating that the specimen is a mature female apparently in or near spawning condition. No trace of implanted spermatophores could be seen in the photos or on the frozen specimen at sites where spermatophores normally are implanted on other octopoteuthids, e.g., on the head, around the neck or just inside the mantle cavity.

Bermuda Specimens.

The Ocean Acre Program was a multi-year sampling program conducted off Bermuda in a 1° square area centered at 32°N 64°W (see Gibbs and Roper, 1970 for details). The principal collecting gear was a 3 m Isaacs-Kidd Midwater Trawl with a fine mesh liner and fitted with a multiple closing device, the Discrete Depth Plankton Sampler (Aron *et al.*, 1964).

Sixteen paralarval and juvenile specimens of *Taningia danae* were captured during the Ocean Acre Program, eight of them at discrete depths in the closing chambers. The closing net specimens, 5-15 mm ML, were captured at depths between 55 and 298m, while 6 of the 8 open-net captures, 5-12 mm ML, were taken in 180-0m. Although these catches represent too few data points upon which to prove details of diel migration, the plotted data do show a clear tendency toward gradual ontogenetic descent that begins at less than 10 mm ML (Fig. 7). A reverse diel migration might occur as well, because five of the six nighttime captures are at depths greater than the five daytime captures.

The specimens from off Bermuda were collected during the months of late February, March, June, August and September. Over the five years that the Ocean Acre Program existed (1968-1972), sampling was conducted during all months of the year, so the occurrence of paralarvae during the spring to fall months indicates a long spawning or recruitment season. These records from two distant locations during several years (1968-1972, 1990) and throughout the seasons indicate that *Taningia danae* is a permanent resident in the western North Atlantic.

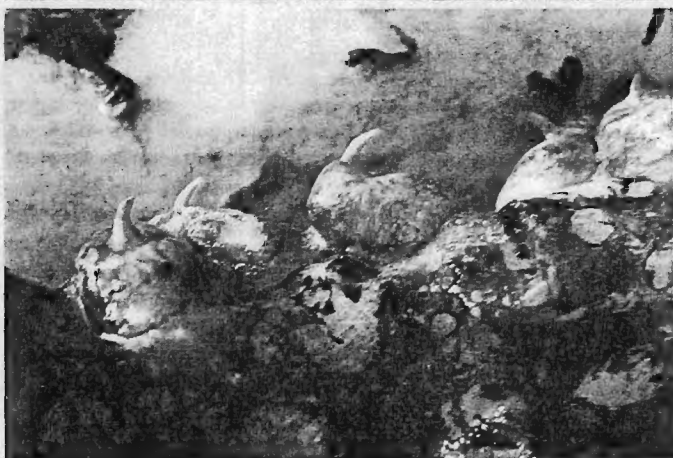
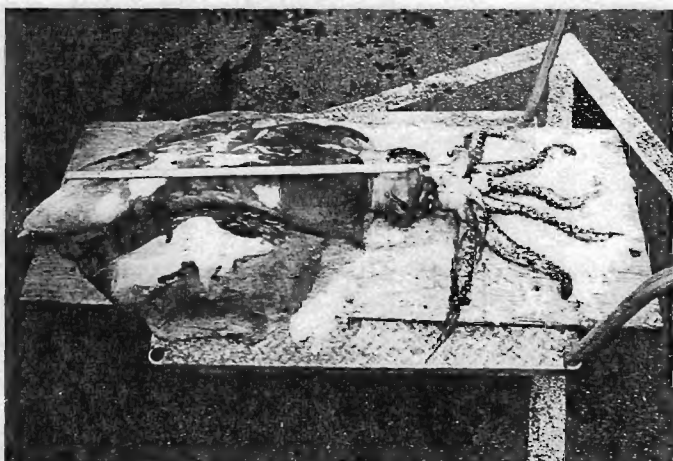


Fig. 1. *Tanningia danae*, Georges Basin specimen, 160 cm dorsal ML, ventral view; scale is meter rule.

Fig. 2. Chitinous hooks on arm of *T. danae*, Georges Basin specimen.

Fig. 3. Mantle of Georges Basin *T. danae* held open to show cream-colored nidamental gland on right, gill on left, funnel with locking mechanism in foreground.

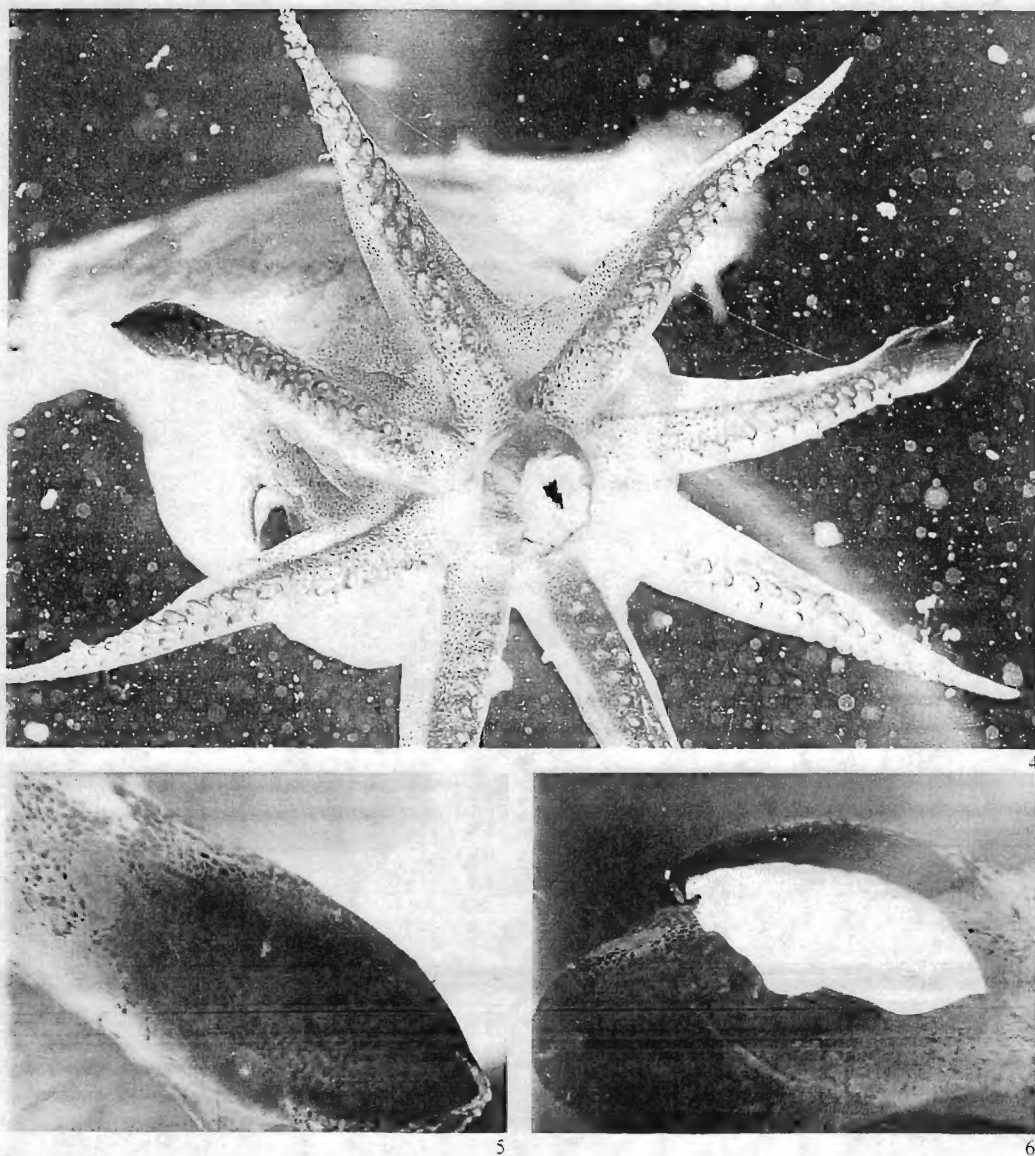


Fig. 4. *Taningia danae*, ca. 6 cm ML, in shipboard aquarium off Hawaii; arms splayed in oral view; note photophores on tips of dorsolateral arms.

Fig. 5. *Taningia danae*, same specimen as in Figure 4, arm-tip photophore (closed); note dark longitudinal seam.

Fig. 6. *Taningia danae*, same specimen as in Figure 4, arm-tip photophore; double-exposed photograph of both closed state and open (flashing state) showing white light-producing surface.

Central Pacific Specimens

In the central North Pacific a specimen of 62 mm ML was taken at 41°N, the most northerly location recorded from the Pacific. The specimen also closes the huge gap in the known distributional range between the other widely separate North Pacific sites just off the coasts of California and Japan.

Finally, two specimens were captured in rectangular midwater trawls from the area of the central Pacific off leeward Oahu, Hawaiian Islands (see Young and Roper (1976, 1977) for details of sampling programs).

Additional Material

The collections in the Smithsonian's NMNH contain several other specimens of *T. danae* not previously recorded in the literature. All were captured with nets, not by predators.

Four separately caught specimens, two each from off Madeira and the Cape Verde Islands, are from the region of the type locality in the eastern North Atlantic where records of *T. danae* abound, mostly from the stomachs of sperm whales.

Four more specimens come from the South Atlantic: one from off St. Helena Island and 3 from farther south, just north of the Antarctic Convergence, at Gough Island and westward off Argentina.

A small specimen was taken east of New Zealand, in the western South Pacific, the first recorded in that area, although specimens are common in sperm whale stomachs from the Tasman Sea to the west of New Zealand.

Bioluminescence.

One of the Hawaiian specimens, approximately 60 mm ML, was alive and in undamaged condition when captured at night, and was placed in a shipboard aquarium for observation (Fig. 4) by R.E. Young and C.F.E. Roper in 1975. The organs on the tips of the dorsolateral arms were thought to be photophores, even by Joubin (1931), but luminescence never had been observed directly in *T. danae*. Therefore, we placed the specimen in a cold water aquarium (5°C) in complete darkness, and the observers' eyes were allowed to adapt thoroughly to the dark. Without the aid of light one observer slowly moved his hand around in the aquarium in an effort to stimulate a response.

Two primary responses were evoked. Both included bright flashes of brilliant blue-green light simultaneously from both arm-tip photophores. The most common reaction involved the coordinate flashes accompanied by an attack, grasping the researcher's fingers and biting. The second reaction was observed clearly once and less dramatically several times. This involved a bright flash followed by rapid retreat from the stimulus. The flashes appeared to vary somewhat in intensity and duration. Usually the flashes lasted only a fraction of a second, but occasionally the organs glowed with fluctuating intensity for 1-7 seconds. These prolonged glows were associated with continuous stimulation, such as pinching the fins. During these prolonged glows the intensity of light appeared to increase gradually to a peak and then it receded gradually.

In addition to the arm-tip photophores, one photophore was located on each side of the intestine, ventral to the ink sac. These organs were observed to glow continuously for periods in excess of 15 min. This illuminated a broad circular area in the mantle cavity and resulted in a general glow ventrally over the entire central dense part of the visceral mass. When the squid was moribund it expanded the chromatophores on the mantle except for a circular patch ventral to the visceral glow.

The specimen was removed from the observation aquarium and the arm-tip photophores examined under a dissecting microscope. Inactive, the bulbous organs were darkly pigmented, unsculptured, integumentary swellings with a dark longitudinal line or seam along the oral surface (Fig. 5). When the animal was stimulated, the seam instantly opened laterally like an eyelid, exposing the yellowish, crenulate surface of the light-producing organ (Fig. 6). Under faint red light, the yellowish coloration of the surface was briefly apparent before being overwhelmed by the blue-green luminescence. However, when the red light was extinguished it was apparent that the luminous surface was emitting a faint glow. Under white light the luminous surface was a brilliant lemon yellow.

Discussion

Bioluminescence.

Observations on bioluminescence in *T. danae* suggest several possible functions. The bright, quick arm-tip flashes startled the observers and created the impression that the flashes serve to startle, distract and confuse an approaching predator. How effective this is on smaller predators can only be imagined at this time. Clearly large predators are not always foiled, because they are by far the largest source of

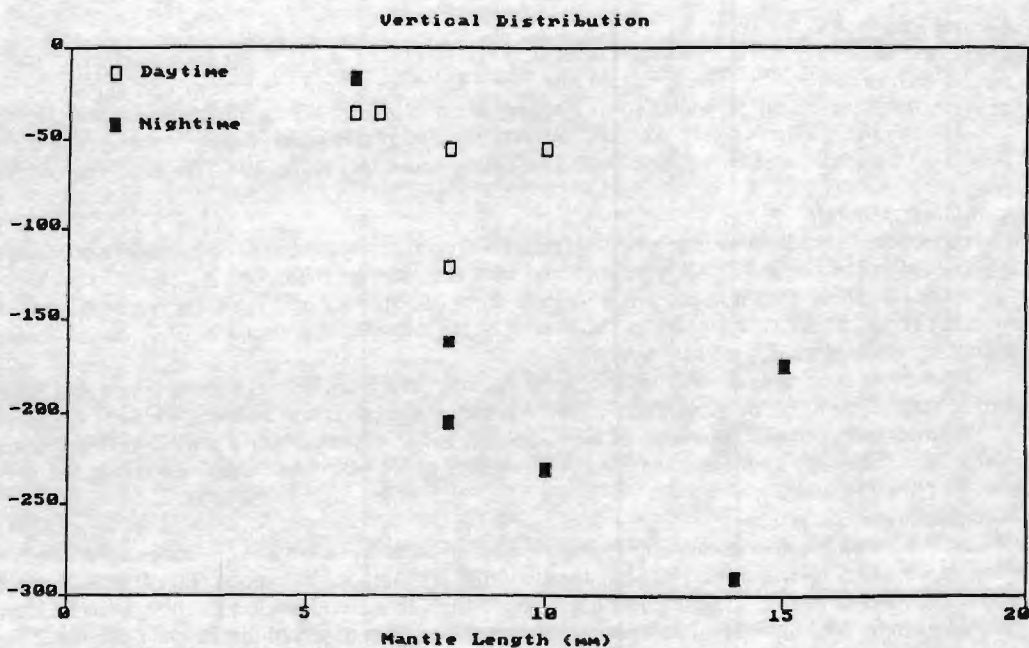


Fig. 7. Vertical distribution of young *T. danae* captured in discrete-depth samples taken with closing nets, showing ontogenetic descent. Data presented in Table 1.

specimens of *T. danae* in collections. These predators include visual hunters such as tunas and lancetfishes. Perhaps because sperm whales hunt using sonar rather than vision, flashing by *T. danae* is a particularly ineffective defense against these predators. Alternatively, flashing may serve as an offensive behavior that disrupts defenses of prey much as Young *et al.* (1982) described for luminescent flashing by *Pterygioteuthis* spp. The function of the visceral photophores that glow through a clear patch in the ventral mantle undoubtedly is a counterilluminating mechanism (Young and Roper, 1976; 1977).

Areal Distribution.

The records of geographical distribution are heavily biased toward regions where sperm whale fisheries occur(ed) and stomach contents were sampled. The records of distribution for *T. danae* are listed in Table 1 and summarized in Fig. 8. The first extensive account of *T. danae* (Clarke, 1967) reported 14 specimens, 10 from sperm whales taken in the southwestern Indian Ocean off Durban, South Africa and four from the eastern Atlantic: Joubin's holotype (Cape Verde Islands), a small juvenile from the Gulf of Guinea, and two from sperm whales (Azores, Madeira). Additional early records in the eastern Atlantic, all listed as *Cucoteuthis unguiculata*, comprise 43 specimens from sperm whales caught off the Azores (R. Clarke, 1956), one large brachial crown found floating at the surface off Madeira (a probable regurgitation from a sperm whale; Rees and Maul, 1956) and one very large specimen from a sperm whale (Clarke 1962a, 1962b-beaks; the same specimen is detailed in Clarke, 1967).

An interesting record of a large specimen of *T. danae* (estimated weight 50 kg) is reported by Clarke and Merrett (1972) from the stomach of a large, bottom living shark, *Centroscyllium coelelepis*, caught on a bottom-set long line at a depth of 1246 m off the Azores. A sperm whale captured southwest of Vigo, Spain (off the coast of northern Portugal—41°32'N, 09°48'W) contained beaks of *T. danae* that numerically accounted for 14.3% of all cephalopod beaks but an estimated 83% of all cephalopod flesh (Clarke and MacLeod, 1974). Although *T. danae* was reported from stomachs of sperm whales caught off Iceland (ca 65°N), an estimated 24% of total weight of cephalopods eaten, Clarke and MacLeod (1976) speculated that the specimens probably were eaten "rather to the south" (p. 742), as beaks can remain in whale stomachs for several days after ingestion. No net-captured specimens of *T. danae* have been reported from north of 53°N (Lu and Clarke, 1975a); one specimen of 0.68 cm ML was caught at night at 25–10m at 53°N 20°W (Lu and Clarke, 1975a). Whereas Mercer (1968) included *T. danae*

in a list of species from Canadian waters, no information for taxonomic verification or locality data were provided.

Small specimens of *T. danae* have been captured by nets in the eastern Atlantic, four (0.5–1.75 cm ML) at 30°N, 23°W in closing nets at 203–102m during day and 300–205m at night (Clarke and Lu, 1974) and two (0.63 cm ML) at 11°N, 20°W also in closing nets during daytime at 50–23m (Lu and Clarke, 1975b).

Larger specimens have been taken from sperm whale stomachs northeast of Tristan da Cunha around 32°S (Vovk *et al.*, 1978) and Nesis (1974) reported a paralarva from southwest of Tristan da Cunha (41°S 26°W). The southernmost records of *T. danae* in the eastern Atlantic are those from the sperm whale fishery off Donkergat, South Africa. The 828 beaks taken accounted for only 1.6% of all beaks analyzed; one buccal mass also was reported (Clarke, 1980).

Reports of *T. danae* from the western South Atlantic are sparse. A sperm whale stranded at Rio Grande do Sul, Brazil (32°25'S, 52°15'W) contained seven beaks that accounted for an estimated 22% by weight of the cephalopod flesh in its stomach (Clarke *et al.*, 1980). Sperm whales captured far offshore from Brazil in the region of 27°–31°S, 32°–33°W contained the flesh of two *T. danae* (Clarke, 1980).

Farther south, beaks of *T. danae* were among the regurgitation of wandering albatross chicks (*Diomedea exulans*) on Bird Island, South Georgia (53°S, 38°W), amounting to an estimated 5.5% by weight of cephalopods fed to chicks by their parents (Clarke *et al.*, 1981). The source of this deep-living species to the surface-feeding albatross was somewhat of a mystery to Clarke *et al.* (1981) who speculate that the cephalopods might come from sperm whales that vomit periodically to rid themselves of accumulated squid beaks or during chase and capture when hunted. An alternative explanation is that this is an example of polar emergence; species that are bathypelagic at lower latitudes are sometimes found near the surface in polar regions (e.g., the bathypelagic cirrate octopod *Cirrothauma murrayi* was reported by Roper and Brundage (1972) to have been dipnetted through a hole in the ice in the Arctic Ocean).

South Georgia has been a center for the Antarctic whaling industry through much of this century. Prey accumulated over many years from sperm whale stomachs were analysed by Clarke (1980), who reported that *T. danae* beaks comprised nearly 11% of total beaks taken from whales in the region of South Georgia but only 0.7% from the rest of Antarctica. The flesh of four specimens also was reported, indicating that *T. danae* occurs, at least in small numbers, south of the Antarctic Convergence.

Records of *T. danae* from the Indian Ocean are primarily from regions where the sperm whale fishery has yielded stomach contents. In addition to those listed above from Clarke (1967), five more specimens are recorded by Clarke (1980), along with 1,577 lower beaks. At the extreme southeastern edge of the Indian Ocean, another sperm whale fishery has been centered at Albany, Western Australia. From there, Clarke (1980) reported flesh of seven specimens plus 83 lower beaks that accounted for just over 3% of all beaks taken. Nesis (pers. comm.) collected two paralarvae south of Madagascar.

Farther to the east in the Great Australian Bight, Zeidler (1981) reported on three large specimens of *T. danae* found floating dead at the surface by fishermen about 120 km offshore from Port Lincoln, South Australia. One specimen was not retained, but the other two were; one with head and arms missing had a dorsal mantle length of 158 cm and weighed 95 kg, and the other in near-perfect condition was 2.1m total length (ML not given) and 110 kg. These weights seem excessive compared with our specimen of slightly larger size (61.4 kg, 135 lbs) and we suspect that these weights were incorrectly reported as kg instead of lb. The 158 cm specimen is, to our knowledge, the largest *T. danae* reported until the 160 cm specimen we record here from the western Atlantic. Nesis (1979) reported two juveniles (20 and 33 mm ML) from the Great Australian Bight.

The most northerly records in the Indian Ocean are from lancetfish (*Alepisauris ferox*) stomachs, one from northeast of Madagascar and four from the central waters (ca 10°S 85°W) (Okutani and Tsukada, 1988). A single paralarval specimen was taken in a midwater trawl fished at 200–0m above Farquhar Seamount north of Madagascar in the western Indian Ocean (Nesis, 1986).

The vast majority of records from the Pacific Ocean also come from predator stomachs. *Taningia danae* was listed to occur in Japanese waters by Okutani (1973), but no records were given. Subsequently, Okutani and Kubota (1976) described the first record in the western North Pacific, a single specimen of 32 mm ML from the stomach of a lancetfish, from Suruga Bay. Then, Okutani *et al.* (1976) reported on six large specimens from sperm whales taken off northeastern Honshu, the largest of which was 149 cm ML. Eight additional records were reported from sperm whales in the same region and north-

ward (31°–36°N), but they were smaller than the preceding specimens, measuring up to 47.5 cm dorsal ML (Okutani and Satake, 1978). Nesis (1973, 1977, pers. comm.) also collected paralarval specimens from the Kuroshio zone.

Table 1. Records of *Taningia danae* based on literature and specimens reported in this paper.

Location Mantle length, (cm)	Number and Sex	Depth (m)	Capture method	Reference
NE Atlantic				
4.0*	1	0–100	open pelagic	Joubin, 1931
—	43 beaks	—	sperm whale	Clarke, 1956
—	1	0	floating	Rees & Maul, 1956
100–140	1U, 1F	—	sperm whale	Clarke, 1967
—	1 fresh	1246	shark	Clarke & Merrett, 1972
—	10 beaks	—	sperm whale	Clarke & MacLeod, 1974
0.5–1.75	4U	102–300	discrete pelagic	Clarke & Lu, 1974
0.68	1U	10–25	discrete pelagic	Lu & Clarke, 1975a
0.63	2U	23–50	discrete pelagic	Lu & Clarke, 1975b
—	56 beaks	—	sperm whale	Clarke & MacLeod, 1976
0.2–12.3	1M, 2F, 1J	0–608	open pelagic	This paper
NW Atlantic				
160	1F	260	open benthic	This paper
8–15	1M, 7J	55–230	discrete pelagic	This paper
5–26	1M, 7J	0–400	open pelagic	This paper
23	1J	—	blue shark	Nesis, pers. comm.
Gulf of Mexico				
1	1U	0–1000	open pelagic	Nesis, 1975
SW Atlantic				
—	2 flesh	—	sperm whale	Clarke, 1980
—	4 flesh, 227 beaks	—	sperm whale	Clarke, 1980
—	7 beaks	—	sperm whale	Clarke <i>et al.</i> , 1980
1.3	1U	0–450	open pelagic	Nesis, 1974
SE Atlantic-				
2.8	1M	0–175	open pelagic	Clarke, 1967
47	1U, 829 beaks	—	sperm whale	Clarke, 1980
—	(number unknown)	—	sperm whales	Vovk <i>et al.</i> , 1978
NE Pacific				
—	1 beak	—	elephant seal	Condit & LeBoeuf, 1984
—	1 beak	—	sperm whale	Fiscus <i>et al.</i> , 1989
NW Pacific				
2.7	1U	0–320	open pelagic	Nesis, 1974
8.5–17	3M, 1F, 2U	—	open pelagic	Okutani, 1974
3.2	1U	—	lancetfish	Okutani & Kubota, 1976
91–149	6U	—	sperm whale	Okutani <i>et al.</i> , 1976
1.2–1.5	3U	0–1000	open pelagic	Nesis, 1977
27–47.5	8U	—	sperm whale	Okutani & Satake, 1978
1.0	1U	0–200	open pelagic	Nesis, pers. comm.
Central Pacific				
6.2, ca 6.0	1F, 1U	0–250	open pelagic	This paper
SW Pacific				
—	1 flesh	—	lancetfish	Rancurel, 1970
—	348 beaks	—	sperm whale	Clarke & MacLeod, 1982
SE Pacific				
1.2–8.0	16U	—	open pelagic	Okutani, 1974
—	3 beaks	—	sperm whale	Clarke <i>et al.</i> , 1976
3.8–5.1	1M, 3U	—	tuna	Okutani & Tsukada, 1988
Central Indian				
3.5	1U, 3 flesh	—	lancetfish	Okutani & Tsukada, 1988

Location Mantle length, (cm)	Number and Sex	Depth (m)	Capture method	Reference
SW Indian				
20-68	1F, 9U	—	sperm whale	Clarke, 1967
36, 60	1F, 1M, 37U, 1577 beaks	—	sperm whale	Clarke, 1980
—	1J	0-200	open pelagic	Nesis, 1986
1.6-2.0	2U	0-200	open pelagic	Nesis, pers. comm.
SE Indian				
—	7 flesh, 83 beaks	—	sperm whale	Clarke, 1980
Great Australian Bight				
2.0-3.3	2U	0-1300	open pelagic	Nesis, 1979
158	1U	0	floating	Zeidler, 1981

*: Mantle length estimated by measuring illustration in original description; F: Female; M: Male; U: Unsexed; J: Juvenile; Beaks: lower beaks only; Flesh: any specimen with soft tissue, e.g., buccal mass, arm crown, whole specimen; floating: Specimen found dead at the surface.

Rancurel (1970) recorded the first *T. danae* in the Pacific Ocean. It was a brachial crown found in the stomach of a lancetfish caught at 27°07'S, 178°16'W (misprinted in Rancurel as 27°07'N), west of the Kermadec Islands. Subsequently, a large number of *T. danae* have been reported from farther to the southwest in the Tasman Sea, ranging from north of New Zealand southwestward to off Tasmania (Clarke and McLeod, 1982). A total of 348 *T. danae* lower beaks and flesh (33% of total number of cephalopod remains) accounted for an estimated 42% by weight of all cephalopods consumed by sperm whales, just over twice the weight of the next species, *Kondakovia longimana*. Sixty-four of the 66 sperm whales sampled (97%) had remains of *T. danae*.

In the southeastern Pacific, sperm whales captured off northern and central Peru had beaks from three specimens of *T. danae* (Clarke *et al.*, 1976). The eastern tropical Pacific cephalopods were intensively studied by Okutani (1974) who recorded 16 specimens of *T. danae* that ranged from 1.2 to 8 cm in ML; all were captured in a 5' × 5' EASTROPAC micronekton net. In the same region four additional specimens 3.8-5.1 cm in ML were taken from the stomachs of tunas (species not stated; Okutani and Tsukada, 1988).

Okutani (1974) also recorded *T. danae* taken in a variety of midwater nets from farther north in the California Current (ca. 30°-40°N). The specimens ranged from 8.5 to 17.0 cm ML, the largest of which was reported to be a gravid female with numerous spermatophores attached. This seems to be quite a small specimen of *T. danae* to be sexually mature, as the largest ones known, up to 160 cm ML, are also mature females. However, because some of the specimens reported in that paper may be *Octopoteuthis* (e.g. fig 14a) it is possible that the gravid female is in fact an *Octopoteuthis*. Alternatively, this size difference may indicate a second species of *Taningia*, but thorough study based on much additional material is necessary. Additional records from off California include one lower beak from a sperm whale (37°-33°N) (Fiscus *et al.*, 1989) and one from the stomach of an elephant seal (*Mirounga angustirostris*) (Condit and LeBoeuf, 1984).

With the addition of the material presented in this paper, the geographical distribution of *Taningia danae* can be described as truly cosmopolitan with the exception of polar regions. It occurs in all major ocean basins: in central waters, near oceanic islands, near continental slopes. It occurs in warm, temperate, and sub-boreal waters.

Cosmopolitan Species.

Truly cosmopolitan species of cephalopods are quite unusual. In fact, cosmopolitanism frequently is ascribed to species that are not well known systematically across their entire geographic range. When sufficient material becomes available, systematic analysis reveals that the supposed cosmopolitan species is, in fact, a complex of closely related species. We are unable to predict at this stage of knowledge whether this will turn out to be the situation for *Taningia danae*, but we don't rule out the possibility. Clarke and MacLeod (1982) remarked that a second species might occur based on their observations of two consistent size classes of lower beaks, although this might indicate developmental cohorts. The small mature female reported by Okutani (1974) from the California Current likewise might represent

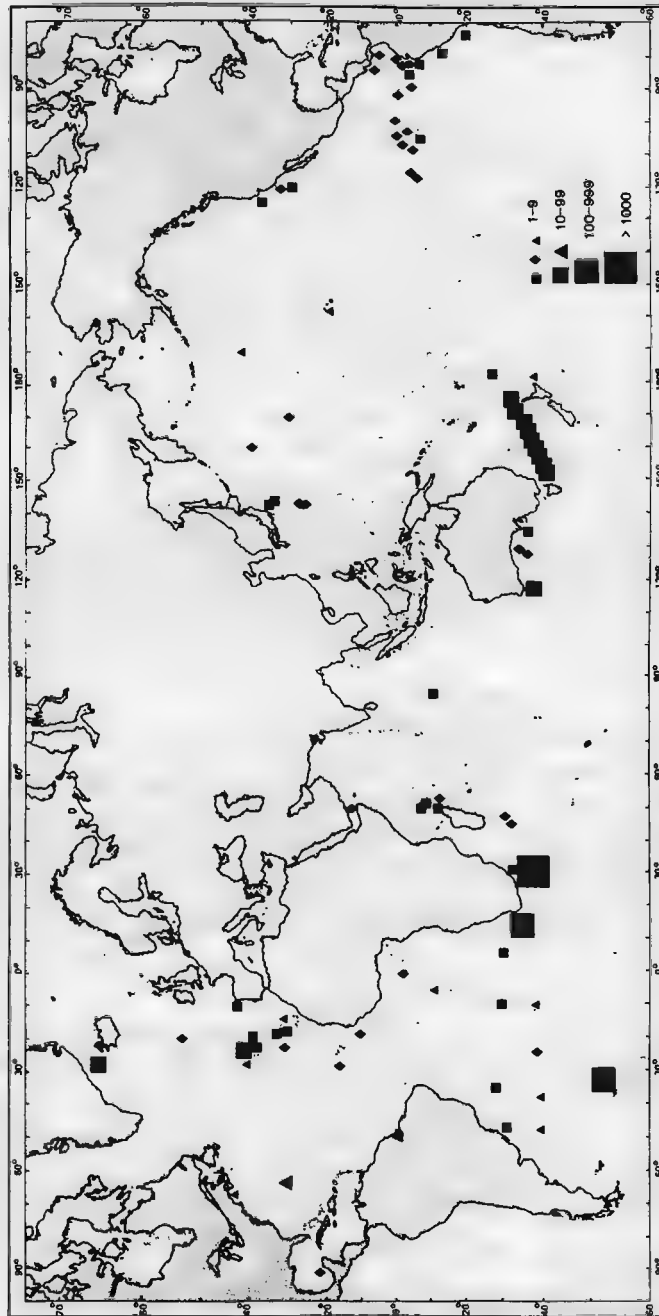


Fig. 8. Geographical distribution of *T. danae*. Triangles: specimens reported in this paper; diamonds: literature reports of specimens collected by nets; squares: literature reports of specimens from stomach contents of predators or found floating (presumably regurgitated by predators).

a separate species (but see comments above about possible misidentification). However, for the sake of nomenclatural stability and until broad-based collections of whole animals become available, we believe that the specific designation for *Taningia* should remain the single species *danae* Joubin, 1931.

Vertical Distribution.

The vertical distribution of *T. danae* also extends over a broad range. Our closing net data indicate an ontogenetic descent, in which smallest specimens occur close to the surface, the upper 100m or so, and increasingly larger animals occur at increasingly greater depths (Fig. 7). Although it is difficult to assess depth of feeding by predators such as sperm whales, the species composition in their diets indicates that whales feed primarily on bathypelagic and bathybenthic species (Clarke, 1977). Sperm whales regularly feed at depths in excess of 1,000m (Clarke, 1977), and the record of a *T. danae* from the stomach of a bottom-dwelling shark caught at 1,248m (Clarke and Merrett, 1972) lead us to suggest cautiously that *T. danae* occurs at these depths. But we emphasize that inferences on depth distribution drawn only from predator-prey interaction can be misleading (see discussion in Roper and Young, 1972). However, with the exception of a few large *T. danae* found dead at the surface (Zeidler, 1981) (probably regurgitated by whales), larger specimens come from the deep-feeding sperm whales. Now, in contrast, we have the largest *T. danae* recorded, taken alive in a trawl where bottom depth was only 260 m, seemingly very shallow for adults of this species. *Taningia danae* certainly extends over a broad vertical range. The young undergo ontogenetic descent and the adults become benthopelagic, associated with but not restricted to the bottom. Data are insufficient at this time to know if their vertical distribution also has a diel component, as is true of the vertical wanderers (sensu Roper and Young, 1975).

Occurrence in western North Atlantic.

An intriguing question remains to be discussed: Why hasn't *T. danae* been reported from off north-eastern North America until now? This region is one of the most heavily fished areas in the world and biological sampling has been intensive for a century. Over the years, we have had access to thousands of lots of cephalopods, e.g., MARMAP/BLM (Vecchione *et al.*, 1986), Deep Dumpsite 106 (Lu and Roper, 1979), the collections at the National Museum of Natural History and the University of Miami, numerous published lists of cephalopod species from other collections, etc., yet no *T. danae* have been found (with the exception of Mercer, 1968).

The very unusual oceanographic conditions off New England during the year 1990 might account for part of the answer. Water temperatures were well above normal in the summer and fall, and a number of tropical and subtropical species were reported in New England waters (V. Anthony, National Marine Fisheries Service Northeast Fisheries Center, Woods Hole, MA, pers. comm.). For example, large numbers of the tropical benthic *Octopus burryi*, heretofore known only rarely as far north as North Carolina, were observed and collected in Narragansett Bay, Rhode Island (W. Macy, Univ. of Rhode Island, pers. comm.). Furthermore, large specimens of the tropical pelagic fishes, luvar (*Luvarus imperialis*) and opah (*Lampris guttatus*), were reported in waters off New England (B. Collette, National Marine Fisheries Service Systematics Lab., pers. comm.).

Possibly *T. danae* is an occasional visitor to the Gulf of Maine region only during years when warm-water incursions occur, a result of warm core eddies breaking off the northwestern edge of the Gulf Stream. East of the Gulf Stream, however, *T. danae* must be a permanent resident, as juveniles were captured in each of five consecutive years, 1968–1972, off Bermuda.

Abundance.

The records of *T. danae* are too scattered around the world to enable us to estimate accurately the abundance of this species. If the data from some predators are reliably indicative of abundance, however, then *T. danae* could be extremely abundant at least in some areas. For example, Clarke and MacLeod (1974) estimated that *T. danae* accounted for 83% by weight of squid eaten by sperm whales off northern Portugal and southern Spain. Of course, one 60 kg *T. danae* specimen could provide the biomass equivalent of 30–60 squids of other species commonly eaten by sperm whales. In areas like the Tasman Sea *T. danae* must be readily available, because 97% of the 66 sperm whales sampled there had remains of *T. danae* in their stomachs and this species accounted for an estimated 42% by weight of all cephalopods eaten (Clarke and MacLeod, 1982). In a discussion on estimating biomass of cephalopods using data from predators, Clarke (1983) noted that some species, among them *T. danae*, might exhibit a dramatic increase in abundance (biomass) as populations of its major predator, sperm whales, become reduced through continued whaling. Such a hypothetical populational increase, however, might be academic, as other large predators may crop the excess. Furthermore, populations of squids are likely to be limited by food availability rather than predation.

The evidence indicates that *T. danae* must be a very abundant species. Furthermore, because individuals grow to such a large size, it must contribute significantly to the overall biomass of cephalopods in the ocean.

Postscript: After this manuscript was completed, we learned about an additional record of *T. danae*. A large squid, "nearly five feet long", was stranded on the beach at Tucker's Town Bay, Bermuda on 23 March 1986. The specimen was provisionally identified at that time, but it was not until October, 1991 that we verified it to be *T. danae* through examination of the arm hooks and arm tip photophores, the only parts of the squid that were preserved. These parts are deposited in the Bermuda Aquarium and Museum.

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Note Added in Proof: As the current paper was being edited and typeset, another description of photophores and bioluminescence in *Taningia* was published by Herring *et al.* (1992. J. Zool., Lond. 227: 479-491): These authors examined four specimens (14.0-46.2 mm ML), three moribund and one live and "very active", collected during 1981-86 in the eastern Atlantic (32-37°N, 17-34°W). Their observations on the general morphology and function of the arm-tip photophores were very similar to ours. They also described the histology and emission spectra of these photophores. Although they concluded that the fast flashes indicate direct nervous control of luminescence, it is actually the eyelid-like structure that occludes and exposes the photophore that is under nervous control and produces the brief flashes. Particularly noteworthy, though, was their unambiguous statement that *T. danae* "has only the two greatly enlarged arm tip photophores and lacks all others". This obvious contrast with our observations of functional visceral photophores in a Hawaiian specimen again raises the question of multiple species in the genus. The visceral photophores are difficult to find in preserved specimens and the very limited number of live observations precludes conclusions on the species question at this time.